Transport of Juvenile Gem Clams (*Gemma gemma*) in a Headland Wake

KELLY L. RANKIN¹ Cook College Rutgers University New Brunswick, New Jersey 08903

LAUREN S. MULLINEAUX² Biology Department Woods Hole Oceanographic Institution Woods Hole, Massachusetts 02543

W. ROCKWELL GEYER

Applied Ocean Physics and Engineering Department Woods Hole Oceanographic Institution Woods Hole, Massachusetts 02543

ABSTRACT: Accumulation of bivalve recruits in the bottom convergence at the center of coastal eddies has been suggested as a possible mechanism resulting in locally abundant adult populations. We investigated transport of juvenile gem clams (*Gemma gemma*) in a headland wake to determine whether they accumulated, and where. Velocity measurements during three flood tides showed that a wake consistently formed, but that flow speeds were too slow to transport juvenile clams to the eddy center. Instead, the clams were deposited just inside the wake perimeter, where shear velocities decreased to levels below critical erosion velocities of the clams. This result demonstrated that accumulation in a coastal flow separation can occur even in the absence of a well-defined eddy or a strong bottom convergence. Juvenile gem clams were carried, probably as bedload, to regions in the wake dominated by sediments with similar grain sizes, rather than similar fall velocities, suggesting that bedload transport was particularly dependent on particle diameter in this flow regime. Adult gem clam populations tended to be locally abundant in regions receiving transported juveniles, but clam transport on any specific flood tide was not sufficient to fully predict the adult distributions.

Introduction

Associations between benthic infaunal assemblages and specific hydrodynamic regimes are observed frequently in coastal habitats. Studies of these associations often concentrate on the influence of horizontal velocity and bottom stress on the flux and accumulation of food or colonists (reviewed in Butman 1987). Vertical flows such as those generated at eddies and fronts also have a high potential for accumulating negatively buoyant particles and organisms but have received less study, largely because they are more difficult to measure. The potential for bottom convergences in coastal eddies to accumulate bivalve recruits was recognized by Kellogg (1905; cited in Turner 1953), long before instruments were available to measure the vertical flows. Although sediment sorting and accumulation of zooplankton have been

observed in coastal eddies. (Wolanski and Hamner 1988), and aggregations of early-stage bivalve larvae have been noted in surface convergences (e.g., Jacobsen et al. 1990), few observations exist on seafloor accumulation of benthic recruits by secondary or vertical flows.

Coastal eddies form when the streamlines of currents separate from the coastline at headlands or other topographic discontinuities. The separation is a consequence of the adverse pressure gradient that forms downstream of the topographic feature. If the headland is abrupt, and the water is sufficiently deep, the eddy forming in the headland wake can develop secondary flows (Wolanski and Heron 1984; Geyer 1993). In this situation, the angular velocity of the eddy imposes a centrifugal acceleration, causing water to "pile up" at the edges of the eddy. The additional height of the water column forces water to downwell at the eddy perimeter. Bottom friction causes the angular velocity of the eddy to slow near the seafloor, reducing the centrifugal acceleration. The inward-directed pres-

¹ Present address: Stevens Institute of Technology, Castle Pt. Station, Hoboken, New Jersey 07030.

² Corresponding author and reprint requests.

^{© 1994} Estuarine Research Federation

sure gradient then predominates over centrifugal acceleration, causing water at the seafloor to flow inward and then upward at the eddy center. These upward flows at the eddy center create the bottom convergence where particles that are too dense to follow the vertical streamlines drop out and accumulate. This process is much like the mechanism that causes tea leaves to accumulate at the center of a swirled teacup, and was invoked by Pingree (1978) as a means of forming sand banks near headlands.

Although vertical flows at the bottom convergence of coastal eddies have been the focus of most discussions of biological accumulation at the seafloor, recent observations by Geyer (1993) suggest that secondary flows need not be confined to eddies, but they can develop due to the curved streamlines around an obstacle such as a headland. Such secondary flows may also accumulate negatively buoyant particles or organisms in the wake of the headland. In this alternative scenario, particles near the bottom are advected across streamlines of the main tidal flow toward the axis of flow separation. Particles may be concentrated by the bottom convergence, but they also may drop out of suspension along the transverse velocity gradient, in a region where the velocities decrease to levels below the threshold necessary to keep the particles in suspension. This cross-streamline transport and accumulation can occur in flow separations at headlands (headland wakes) even where a well-defined eddy is absent.

The supposition of Kellogg (1905), that localized, abundant populations of soft-shell clams (Mya arenaria) form under coastal eddies through hydrodynamic aggregation of the larvae and juveniles at the bottom convergences, is intriguing, but no studies have been conducted to verify the mechanism, or to exclude possible alternative causes for a correlation between bivalve aggregations and coastal eddies. We suggest that secondary flows in a headland wake may aggregate benthic organisms, even in the absence of a well-defined eddy. Alternatively, biological processes, such as active migration of bivalve larvae or juveniles into eddies, or enhanced bivalve survivorship and growth due to hydrodynamic enhancement of particulate food flux and accumulation, may also result in local aggregations.

The objective of the present study is to document flows around a headland, and measure transport of the gem clam, *Gemma gemma*, to determine whether hydrodynamic transport of the clams causes them to accumulate in the wake of the headland. *G. gemma* is a suspension-feeder and is dioeceous and oviviparous, so it does not have a planktonic larval stage. We chose this species to

test the "passive accumulation" hypothesis because juveniles do not actively emerge into the water column, nor do they actively swim down toward the sediment. Thus, their transport should be determined by their size, shape, and density, and the hydrodynamic regime, rather than by active swimming. Two alternative hydrodynamic processes (accumulation in the bottom convergence versus accumulation along the transverse velocity gradient) were investigated by measuring velocities in the headland wake, locating the convergence, and determining the fate of transported G. gemma. These observations were then compared to distributions of sediment grain size and adult gem clam abundance to investigate whether young clams were transported as suspended, passive particles (the "passive accumulation" hypothesis; Hannan 1984) and whether transport resulted in local adult aggregations.

During the last few decades, extensive studies have been conducted to evaluate the role of hydrodynamic processes on benthic recruitment. We know that physical transport processes often play an important role in dispersal and settlement of benthic invertebrates with planktonic larvae. Physical processes, however, may continue to influence the distribution of organisms after they have completed their larval stage and settled to the sediment bed. For example, near-bottom currents may erode postlarval and adult organisms from the bed when the bottom shear velocity exceeds the critical erosional velocity for underlying sediments (Palmer 1988). Furthermore, recent field studies have verified that bedload transport may be responsible for the widespread relocation of juvenile soft-shell clams (Emerson and Grant 1991). It has been demonstrated clearly that the distribution of bottom shear stress in coastal habitats has a strong potential for influencing sediment deposition and larval recruitment, and transport of small benthic adults. The present study is designed to expand on these previous investigations by evaluating the relative influences of secondary flows, bottom shear stress gradients, and vertical flows in accumulating juveniles of G. gemma.

Background

The natural history and population dynamics of *G. gemma* were studied extensively during the 1950s and 1960s in Buzzards Bay (Sanders 1958) and Barnstable Harbor (Sanders et al. 1962; Green and Hobson 1970), Massachusetts, and in Union Beach, New Jersey (Sellmer 1967). Initially, these investigators expected that because *G. gemma* had no planktonic larval phase, it was probably transported by waves and currents. Sanders et al. (1962) postulated that the clams should accumulate in de-

positional areas where currents slowed and muds collected. Most of the clams, however, were found to live in well-sorted, fine sands in intertidal and shallow subtidal habitats. This distribution may have been a result of clams dropping out of suspension (or bedload) in flows that were faster than those that deposited muds, but the investigators suggested instead that biological interactions were more important than hydrodynamic transport processes in controlling distribution patterns. Green and Hobson (1970) concluded that transport of the clams by currents and waves was insignificant, but they based their conclusion on low numbers of G. gemma collected in a single 32-cm diameter net that was deployed in the water column for 1 h. Given the more-recent observations of bedload transport of even much larger bivalves (soft-shell clams; Emerson and Grant 1991), we suggest that hydrodynamic transport may have influenced G. gemma in these previous studies, but it was not adequately investigated. Biological processes, however, such as dispersal through burrowing (Jackson 1968), intraspecific competition (Weinberg 1985), and predation (Sellmer 1967) have strong potential influences and cannot be ignored.

In New England, populations of *G. gemma* experience two recruitment pulses: one in June from the overwintered broods and a second in August from the summer broods. The young-of-the-year are generally less than 0.9 mm in diameter, and attain sizes of 1.5–3.5 mm as adults (Green and Hobson 1970). Population densities of adults can become very large, reaching 300,000 individuals m^{-2} in some areas; these were termed *Gemma* flats by Sanders (1958).

Study Site

The study site was located in Little Buttermilk Bay at the opening of Gibbs Narrows, a channel connecting with Buttermilk Bay, Massachusetts (Fig. 1). The region of interest was just downstream of the channel opening (Lewis Point), where eddies were expected to form on the flood tide. Tides were semidiurnal and the average tidal range was approximately 1.2 m (Fish 1987). The site comprised a sandspit that was partially exposed during low tide, and a deeper muddy embayment with a maximum depth of 1.8 m at mean low water.

The site was chosen because its hydrography and bathymetry had been previously studied (Fish 1987), its size was suitable for a field study, and scaling considerations indicated that formation of an eddy with a bottom convergence was highly probable during flood tides. Coastal eddies are expected to form when three criteria are satisfied: the headland, or other topographic discontinuity, has a large aspect ratio (a:b, where a is length and



Fig. 1. Location of study site near Lewis Point in Little Buttermilk Bay, Massachusetts.

b is width); the tidal excursion $(2U/\sigma, \text{ where U})$ is tidal amplitude and σ is tidal frequency) is large in comparison with the width of the headland; and the frictional length scale (h/2C_D, where h is water depth and C_D is the depth-averaged drag coefficient) is at least as large as the width of the headland (Signell and Geyer 1991).

Estimates of each of these scaling factors can be made for the flood tide in Little Buttermilk Bay. The "headland" responsible for steering the flow during most of the tidal cycle is the sandspit extending from the channel opening; it is 50 m long and 10 m wide, resulting in an aspect ratio (a:b) of 5. The tidal excursion is more than 1,000 m, calculated for a typical tidal current of 0.1 m s⁻¹. And the frictional length scale is approximately 83 m (h = 0.5 m and $C_D = 3 \times 10^{-3}$), where the depth-averaged drag coefficient is within the range of those commonly used for shallow coastal environments (e.g., Bowden 1981). These estimates are all within the range for eddy formation (Signell and Gever 1991).

Scaling arguments were also used to evaluate the probable intensity of secondary and vertical flows. Based on results of Kalkwijk and Booij (1986) and Geyer (1993), horizontal convergence velocities could reach approximately 20% of main streamwise tidal flows. Using a main streamwise tidal velocity of 0.2 s⁻¹, we calculate an expected convergence velocity of approximately 4 cm s⁻¹. Although vertical velocities are likely to be quite small in this flow (on the order of 0.01 cm s⁻¹, based on scaling arguments), they may be significant for accumulating biological particles with comparable settling velocities.

Materials and Methods

The location and general size of eddies forming on flood tide near Lewis Point (where Gibbs Narrows opens into Little Buttermilk Bay) were determined qualitatively by tracking the paths of umbrella-shaped Woodhead sea-bed drifters. Results of three releases of 20 drifters indicated that an eddy did indeed form on flood tides, and that near-bottom currents curved in toward the eddy center, as expected for a bottom convergence (Mullineaux et al. in prep). These data were used to design the sampling array, a 200 m \times 200 m grid oriented along the axis of the sandspit. Sampling locations within the grid were marked with buoys at 50-m intervals (Fig. 2). Velocities in the eddy were measured with an S4 electromagnetic current meter, suspended 0.5 m above the seafloor on a mooring. The current meter was deployed for 5-min intervals at each grid station during peak flood tide on three occasions, July 2, 16 and 25, 1991. Velocity sampling was initiated 2 h after slack tide and continued over the following 3 h. Since the measurements were taken sequentially, rather than synoptically, the sampling of grid stations was done in random order (except for a few shallow sites that could be sampled only when the tide was sufficiently high) on each sample date.

Mid channel velocity measurements were recorded southwest of station A1 at a height of 1.5 m above bottom on May 10, September 21, and September 22, 1991. The records on May 10 spanned the transition from ebb to flood tide; those on September 21 and 22 covered the flood tide for 5 h, 34 min and for 4 h, 45 min, respectively.

All velocities measured within the grid were later adjusted to peak flood to correct for the effects of sequential sampling. Adjusted velocities were calculated assuming sinusoidal variation in tidal velocity over the 6-h flood tide:

$U_c = U_m / \sin \sigma t$

where U_c and U_m were the corrected and measured velocities, respectively, σ was the tidal frequency, and t the time elapsed from slack. A time correction was made to the published commencement of the flood tide (National Oceanic and At-



Fig. 2. Grid of sampling locations near Lewis Point. Solid line shows bathymetry (0.5 m); dotted line indicates contour of sandspit exposed at mean low water.

mospheric Administration Nautical Chart 13229, 1990) because of the lag caused by the shallowness of this particular bay. This time correction was arrived at from mid-channel velocity records, measured on May 10, 1991, showing that the shift from ebb to flood tide occurred 28 min after the predicted shift.

The transport rate of *Gemma gemma* was measured simultaneously with flood-tide velocity measurements. Collection trays for *G. gemma* were constructed from 15.3 cm diameter PVC pipe. A circular bottom was cut for the trays from sheet PVC and was cemented into the core 0.5 cm from the top. Transport rates were calculated from the number of individuals that accumulated in the 184 cm² area of the tray over the duration of the flood tide. Immediately before deployment, trays were filled with ambient sediment collected and frozen from the study site in the spring of 1990, before the first spawn. This sediment was relatively free of bivalve shells, and any remaining were gaping and

easily differentiated from live *G. gemma* collected in samples. Each tray was labeled and placed by divers flush with the sediment to avoid flow disturbances. Lids were kept on the trays until all trays were buried, then the lids were removed allowing bivalves access to the trays. Sampling was done on the flood tide over a period of 6 h and trays were recovered just before slack tide.

Divers retrieved the trays by slowly replacing the lids in order to minimize disturbance and returned to the surface. Care was taken to retain all of the contents of the tray during its ascent. The samples were immediately preserved in 4% buffered formaldehyde. Forty-eight hours later each sample was washed through a 170- μ m sieve and transferred into 90% ethanol to which rose-bengal dye had been added. Enumeration of *G. gemma* was obtained by sorting through the sediment under a dissecting microscope.

Sampling for background abundances of adult G. gemma was conducted on 4 October 1991. Cores were taken by pushing 3.5-cm diameter PVC pipe into the sediment to a depth of 4 cm. Six replicate push cores were taken at random locations within a 1 m \times 1 m area at each grid station. Each core was placed in a sample jar and preserved with 4% buffered formaldehyde. Samples were later transferred into 80% ethanol, stained with rose-bengal, and examined for G. gemma individuals under a dissecting microscope. Most of the individuals collected in these late-season samples were larger than those transported in the July experiments. The few small specimens (<1 mm in diameter) collected in these push cores were excluded from analyses of resident adults.

Sediment grain-size analyses were conducted to determine sediment fall velocities for comparison with those of juvenile G. gemma. On October 5, 1991, sediment cores 10 cm in depth were taken with care to preserve the integrity of the surface sediment layer. Cores were quickly sealed using plastic caps and later frozen. Sediment analyses were conducted on these cores according to the standard methods described in Folk (1974). A 30-g subsample of the top 2 cm of sediment from each core was removed. Using distilled water, each subsample was wet-sieved through a 63-µm sieve to remove the silt-plus-clay fraction. This fraction was then placed in a preweighed beaker and oven dried at 125°C for 20 h. The sand fraction remaining on the 63-µm sieve was carefully washed with distilled water into another preweighed beaker and dried at 125°C for 20 h. Both the sand fraction and the silt-plus-clay fraction were weighed once again after cooling to room temperature. The sand fraction from each sample was then sieved into different size classes by using a Ro-Tap Shaker for 10 min. The sieve mesh sizes were 2.00 mm, 1.00 mm, 500 μ m, 250 μ m, 125 μ m, and 63 μ m in diameter. Weights of each sand fraction were recorded after the samples were carefully removed from the sieves and placed in preweighed beakers.

Fall velocities (w) for preserved G. gemma were obtained by recording the speed of individuals as they sank through a viewing chamber filled with filtered seawater at room temperature. Following the methods detailed in Hannan (1984), single gem clams were introduced into the water using a micropipette. Care was taken to avoid imposing additional downward momentum on the specimens. Five individuals were randomly selected from each of the two size classes transported into the sediment trays: young-of-year (mean diameter = 0.53mm; SD = 0.066; n = 9), and juveniles (mean diameter = 1.02 mm; SD = 0.14; n = 8). The paths of these sinking clams were recorded on video, and fall velocities were calculated by measuring the distance an individual had settled over a 1-s interval.

Results

CURRENTS

Velocity means measured by the S4 current meter indicate that a headland wake did occur during the flood tides of all sampling dates (Fig. 3). The flow separation was characterized by a strong transverse velocity gradient across the sampling region between the tidal channel and the shoal. A slow return flow was observed near the shoreline (stations B3 and C3), indicating that a small, weak eddy formed close to shore. The orientations of velocity vectors on the first two dates (July 2 and 16) indicate that the eddy center was located in the region of stations B2, B3, C2, and C3. The lowest velocities were recorded near the center of the eddy, and the highest velocities at stations near the channel (Gibbs Narrows). On July 25 the eddy center had shifted downcurrent toward the region bounded by stations C3, C4, D3, and D4. Because of the strong transverse shears, secondary flows (which are not evident in these mid-depth velocity vectors) may be substantial along the outer perimeter of the wake, but are likely to be quite weak within the eddy itself.

Velocity measurements taken on July 16 were much higher than those from the other two sampling dates. These velocities were recorded with a different S-4 current meter that had apparently been miscalibrated. We believe that the speeds recorded by this current meter were not a true indication of the currents on that day because currents did not seem unusually strong to divers working in the grid, and because some of the velocities measured in the headland wake were high-



Fig. 3. Velocity measurements (5-min means) recorded from an S4 current meter moored 50 cm above bottom on July 2, 16, and 25, 1991. Orientation of arrow denotes current direction, length denotes speed. Values for July 16 are corrected for current meter miscalibration (see text).

er than any of our measured channel velocities, and higher than most of the channel velocities measured by Fish (1987). To correct these measurements, we assumed the calibration error was linear, and estimated an upper bound to the velocities by comparing the tidal height on July 16 (4.3 ft) with that on July 2 (3.4 ft) and July 25 (3.4 ft). We assumed that a 26% elevation in tidal height on 16 July corresponded to a similar increase in volume flux, and a consequent 26% increase in channel velocity. Note that we assumed that the bay shoreline was vertical and that the water depth in the channel was constant-these assumptions are not realistic, but they are conservative and result in an upper bound estimate of channel velocity. Thus velocities at the station nearest the channel (C0) on 16 July should have been no greater than 1.26 times those recorded on July 2 or 25. Choosing the stronger velocity from these latter two dates (20.3 cm s⁻¹ on July 25), we estimated that the velocity on 16 July should have been no greater than 25.6 cm s⁻¹. This correction term, 48% of the measured velocity, was used to correct all of the 16 July velocity measurements. The absolute velocities of these corrected measurements should be treated as coarse estimates, but the directions and relative speeds within the grid are useful for locating the eddy center and quantifying relative differences in velocity among stations.

Shear velocity (u_*) at each grid station was calculated from the velocity at 50 cm above the bot-

tom (U_i ; Table 1) using the following equation for turbulent flows (Clauser 1956):

$$u_* = C_D^{\nu_2} \times U_z$$

A value of $C_D = 3 \times 10^{-3}$ was selected as a typical value for coastal environments (Bowden 1981). Critical erosional velocities u*crit for G. gemma were obtained for young-of-year and juveniles from a Shields diagram (Graf 1971), using the measured fall velocities (w) and diameters for the two size classes (Table 2) and estimated specific gravities. Although specific gravities of gem clams were not measured, we expect them to be more dense than planktonic larval bivalves (1.25-1.4 g cm⁻³; S. Gallager unpublished data) because their shells are more heavily calcified and are less dense than sand grains (2.65 g cm⁻³). Calculations of u_{*crit} are not highly sensitive to differences in specific gravity in this range, and varied only from 0.89 cm s⁻¹ to 1.1 cm s⁻¹ for young-of-year G. gemma and 1.15 cm s⁻¹ to 1.3 cm s⁻¹ for larger juveniles.

The mean mid-channel velocity during a complete flood tide interval (5 h, 34 min) on September 21 was 38.9 cm s⁻¹, and shear velocities exceeded the upper limit of critical erosional velocities (1.3 cm s⁻¹) of both size classes of transported *G. gemma* during most (4 h, 35 min) of the flood tide. Mean velocities during portions of the flood tide on May 10 (34.4 cm s⁻¹) and September 22 (28.1 cm s⁻¹) were lower but still strong enough to resuspend gem clams for more than $\frac{1}{2}$ of the recorded intervals. For comparison, mean flood-

TABLE 1. Values for abundance of *Gemma gemma* transported into trays, abundance of resident adult *Gemma gemma* in push cores, current velocity, shear velocity, percent abundance of 1Φ , 2Φ , and silt-clay grain size classes in push cores, and distance from the channel for each station in the sampling grid.

	Transported Gemma (cm-2)		Resident Gemma	Current Velocity (cm s ⁻¹)		Shear Velocity (cm s ⁻¹)			1db	oth	Siluchar	Channel		
Station	July 2	July 16	July 25	x (SD)*	July 2	July 16	July 25	July 2	July 16	July 25	(%)	(%)	(%)	Dist. (m)
Al	2.39	1.21 *	1.02	2.29 (1.53)	5.6	4.7	21.5	0.31	0.26	1.18	30.1	54.4	1.2	75
B1	1.46	0.65	1.24	4.30 (3.40)	8.5	3.3	21.9	0.46	0.18	1.20	32.5	25.0	3.3	75
B2	0.23	0.97	0.63	1.32(0.22)	1.7	2.3	5.6	0.09	0.13	0.29	23.4	41.4	1.0	125
B3	0.07	0.40	0.07	1.69 (0.51)	3.0	7.5	10.8	0.16	0.41	0.59	31.9	37.9	6.6	175
C0	0.00	0.00	0.01		19.5	25.6	20.3	1.07	1.40	1.11	-	_	_	25
CI	3.48	-	0.29	2.04 (1.14)	10.6	19.8	15.6	0.58	. 1.08	0.85	33.9	20.7	1.7	75
C2	2.19	0.17	0.33	2.08 (0.79)	4.5	3.0	5.7	0.25	0.16	0.31	32.8	41.2	3.4	125
C3	0.17	0.15	0.05	0.63 (0.48)	1.3	3.5	2.5	0.07	0.19	0.14	26.4	40.3	12.2	175
D1	1.46	0.20	1.35	2.81 (0.83)	6.4	6.3	5.6	0.35	0.34	0.30	33.6	14.0	1.6	75
D2	_	0.02	0.19	0.66 (0.37)	10.7	9.6	2.5	0.59	0.52	0.14	19.7	34.2	9.2	125
D3	1.03	0.03	0.00	0.52(0.42)	5.3	14.0	3.9	0.29	0.77	0.21	9.6	45.9	15.7	175
D4	0.00	0.00	0.01		9.1	6.2	3.1	0.50	0.34	0.17	_		-	225
EO	0.73	1.88	0.06		19.7	16.6	3.8	1.08	0.91	0.21	-	-	-	25
E1	3.41	0.93	1.25	6.35(4.64)	10.4	9.4	12.5	0.57	0.51	0.68	38.2	34.1	2.3	75
E2	0.46	0.21	0.05	4.84 (1.84)	9.3	15.2	4.2	0.51	0.83	0.23	28.3	46.9	2.1	125
E3	0.03	0.00	0.00	_	8.7	28.6	5.0	0.47	1.57	0.27	-	-	-	175
E4	-	0.17	0.10	-	7.5	20.4	2.8	0.41	1.12	0.15	-	-	-	225

 $a_{n} = 6.$

tide velocities measured in this channel during 1985 and 1986 ranged from 22 cm s⁻¹ to 52 cm s⁻¹ (Fish 1987). The mean flood-tide shear velocities for the channel are thus expected to fall in the range of 1.0 cm s⁻¹ to 2.3 cm s⁻¹, indicating that *G. gemma* should be resuspended and transported through the channel for a substantial interval of most flood tides.

Peak-flood shear velocities at most stations under the headland wake, however, did not appear to be strong enough to resuspend *G. gemma* individuals once they had dropped to the bottom (Fig. 4). Shear velocities at only a few stations around the wake perimeter were strong enough to resuspend even the smallest (young-of-year) clams. Thus, clams transported along the bottom as bedload should have been deposited just inside the wake perimeter. Even for the extreme case of the smallest clams (w = 1.5 cm s^{-1}) suspended at the surface over the deepest bottom (1.8 m) in the fastest flows (20 cm s⁻¹), the clams should have dropped out of the water column within 20–25 m of the wake perimeter.

GEM CLAM ABUNDANCES

G. gemma was the most abundant bivalve transported into the sediment trays; only a few individuals of other species were collected, and they were excluded from analyses. Since G. gemma are brooded and do not have a planktonic larval stage, all individuals found in the trays had been transported there as bedload or suspended load, presumably through Gibbs Channel from Buttermilk Bay.

Trays sampled on July 2 had highest abundances of *G. gemma* on the sand spit, particularly at stations C1 and E1 (Fig. 5). Many fewer individuals were collected in trays located on the mud flat, and no individuals were collected in the trays closest to shore (B3 and D4). On July 16, trays again yielded higher abundances along the sand spit than in the mud flat, although the highest abundance was closer to the channel (station E0) than on the previous sample date. *G. gemma* abundances in trays deployed on July 25 were also highest at stations on the sand spit, near the channel, and lowest in the mud flat. Abundances of *G. gemma* were higher at

TABLE 2. Measured diameters and fall velocities (mean and SD), and calculated critical erosion velocities (u_{ecit} interpolated from modified Shields diagram) for young-of-year and older juvenile gem clams. Range in u_{ecit} reflects range in specific gravity estimates for clams. Parameters for sediment grains (minima for size class; Yalin 1977) listed for comparison.

Gemma Class	Diameter (mm)	Fall Velocity (cm s ⁻¹)	u _{serit} (cm s ⁻¹)	
Young of year	$0.53 \ (0.066; n = 9)$	1.57 (0.042; n = 5)	0.89-1.1	
Juvenile	1.02 (0.14; n = 8)	2.98 (0.28; n = 5)	1.15-1.3	
1Φ	0.50	8.50	1.63	
2Φ	0.25	2.90	0.67	



662

K I Bankin et al

Fig. 4. Shear velocity for all stations on the Lewis Point grid for July 2, 16, and 25, 1991. Dashed lines designate range of critical erosional velocities for both young-of-year and juvenile *Gemma gemma*. A shear velocity exceeding these critical erosion velocities would be strong enough to transport these individuals.

most stations on July 2 than on the later two dates, and probably represented young-of-the-year released from an early summer brood that had not yet experienced high mortality (Green and Hobson 1970). Abundance patterns of resident adult *G. gemma* measured in push cores taken later in the season (Fig. 6) resembled those of the transported juveniles in that the highest abundances were located generally on the sandspit bordering the channel.

Abundance patterns of G. gemma transported to

each location in the grid were compared to shear velocity distributions for corresponding dates (Table 1) using Spearman's rank correlation coefficient r (Sokal and Rohlf 1969). This nonparametric statistic was chosen because the correlations were not expected to be linear, the data were not always normally distributed, and variables were not independent. Correlations were also calculated for transported G. gemma and distance from the channel, and distribution of resident G. gemma adults. Because multiple regressions were not feasible, the number of pairwise comparisons was restricted to only a fraction of those possible, in order to minimize the problem of multiple testing errors. Although we did not adjust the significance level of correlations from p < 0.05, we adopted a conservative interpretation of significant results.

Abundances of transported *G. gemma* were neither consistently nor significantly correlated with shear velocity. They did, however, have consistently (but not significantly at p < 0.05) higher abundances near the channel (on the sand spit) than further away from it, in the mud flat. Resident adult *G. gemma* tended to have high abundances in the same regions that the juveniles were transported to, but the correlation was significant only for the flood tide of July 25.

SEDIMENT ANALYSES

Abundance patterns of G. gemma were also compared to distributions of selected size classes of sediment to determine whether the clams were transported and deposited as passive particles with similar fall velocities or sizes. The 2Φ size class (0.25-0.50 mm diameter grains) was of particular interest because the fall velocities (approximately 2.9-8.5 cm s⁻¹, Yalin 1977) and critical erosion velocities $(0.67-1.63 \text{ cm s}^{-1})$ overlapped those of the juvenile gem clams. The 1Φ size class (0.50–1.00 mm) included grains closest to the diameter of the juvenile gem clams but with substantially larger fall velocities (>8.5 cm s^{-1}). The silt-clay fraction (<63 µm) was also examined because previous research (Sanders et al. 1962) suggested that gem clams may actively avoid these sediments. As expected, the percentage of grains in the silt-clay fraction was highest in the mudflat (stations C3 and D3) and the percentage of the coarsest grains (1Φ) was highest on the sand spit (stations B1, C1 and D1) (Table 1; Fig. 7). Unexpectedly, this coarse size (1Φ) was the only sediment fraction with a consistent (and significant) positive correlation with transported juvenile and resident adult G. gemma (Table 3). The salt-clay sediment fraction tended to be negatively correlated with transported juvenile clams, but the correlation was significant on only one date (July 16).



Fig. 5. Abundance of *Gemma gemma* (individuals cm⁻²) transported into trays during flood tides of July 2, 16, and 25, 1991. Sampling stations missing from grid indicate unrecovered trays.



è

Fig. 6. Abundance of resident adult Gemma gemma (individuals cm^{-2}) collected in push cores on October 4, 1991.



Fig. 7. Percentage of 1Φ grains in sediment collected on October 5, 1991.

TABLE 3. Spearman's rank correlation coefficient, r, and number of measurements (n) for selected pairwise comparisons of transported *Gemma gemma* (on July 2, 16, 25), shear velocity, distance from the channel, resident adult *Gemma gemma*, and percent abundance of 1Φ , 2Φ , and silt-clay sediment grain size classes.

	u. July 2	u. July 16	u. July 25	Channel Distance	Resident Gemma	1Φ	2Ф	Silt-Clay
Gemma July 2	0.07 (15)			-0.45 (15)	0.48 (11)	0.69 ^a (11)	-0.25 (11)	-0.34 (11)
Gemma July 16		-0.34 (16)		-0.47 (16)	0.56 (11)	0.40 (11)	0.15 (11)	-0.79^{a} (11)
Gemma July 25			0.47 (17)	-0.46 (17)	0.63^{a} (12)	0.66^{a} (12)	-0.48 (12)	-0.64 (12)
Channel distance						-0.68° (12)	0.44 (12)	0.68^{a} (12)
Resident Gemma						0.67^{a} (12)	-0.33 (12)	-0.49 (12)
^a p < 0.05.	12				1 S	1.00		

Discussion

The main objectives for this project were to characterize the transport of immature gem clams (G. gemma) in the secondary flows of a headland wake, and to distinguish whether the clams accumulated in a bottom convergence or were deposited along a transverse velocity gradient. The question of whether this transport process enhanced recruitment and was responsible for localized aggregations of adults (i.e., Gemma flats) was also addressed through comparisons of transport and adult distributions. Although an eddy was documented during three flood tides, the gem clams did not accumulate in the eddy center; instead they accumulated along a sand spit at the periphery of the headland wake. Clearly, processes other than vertical flows at an eddy convergence were controlling the transport and accumulation of gem clams in this region.

Secondary flows in combination with a transverse gradient in velocity (from the wake perimeter to the eddy enter), however, did appear to have a strong influence on the transport of juvenile gem clams and accumulation of adults. We tested the hypothesis that juvenile gem clams were transported in secondary flows and deposited as a function of bottom shear velocity. If this transport process were occurring, we would expect clams entering the wake to be transported inward from the outer perimeter, and drop out and accumulate in regions where bottom shear velocity decreased below the clams' critical erosion velocities. Although no significant correlation between absolute shear velocity and G. gemma transport was detected within the wake, clam transport to the perimeter stations (A1, B1, C0, C1, D1, E0, E1, E2) was significantly higher than transport to the interior stations (all other stations except E3 and E4, which appeared to be outside the eddy) on all three sample dates (one-tailed t-test, p < 0.05; t = 1.84, 1.81, 2.09; Sokal and Rohlf 1969). The consistent (but not significant) negative correlations between distance perpendicular to the channel and transported gem clams were also a probable result of deposition along the transverse velocity gradient. The lack of a strong correlation between shear velocity and *G. gemma* transport was most likely a result of the strong transverse gradient in velocities, which resulted in an abrupt reduction of current speed inward from the wake perimeter. Only in the wake perimeter, even at peak flood, did the shear velocity at the bed consistently exceed the critical erosional velocity for *G. gemma*, so transport within the wake interior would not have been well-predicted by velocity.

These results suggest that very little hydrodynamic redistribution of clams in the wake interior should occur, and that clams collected in the travs were probably advected from other locations in the bay. Comprehensive time-series measurements of velocities in Gibbs Channel were not available, but our own measurements in May and September 1991, and Fish's (1987) records from 1984 and 1985 indicate that shear velocities in the channel were sufficiently strong to erode and maintain in suspension young-of-the-year and juvenile gem clams during a substantial portion of flood tide, even on neap tides. Transport rates of clams into the wake are therefore expected to depend on clam densities and shear velocities upstream from the headland and in the channel. Since the clams were probably not resuspended in the wake (with the exception of a few stations along the perimeter), their transport within the wake was likely controlled by their vertical position in the water column. For instance, clams transported along the seafloor as bedload would be deposited immediately when they encountered shear velocities lower than their critical erosion velocities, but those suspended in the water column would be carried further toward the eddy center as they dropped to the seabed. In order to fully understand and predict hydrodynamic transport of gem clams to the study site, additional information on their source population densities and erosion rates upstream from the site would be needed. Transport rates from external sources could then be compared to reproductive rates of gem clams living at the study site to evaluate the relative impact of hydrodynamic transport on local population dynamics.

If currents were transporting gem clams in suspension, and if flood-tide transport controlled deposition integrated over tidal cycles, we would expect clams to be transported to, and accumulate in, regions where the sediments had similar fall velocities. Clams were not transported in high numbers to locations dominated by sediments with similar fall velocities (the 2Φ size class), instead they were advected to stations on the outer edge of the sand spit, which were characterized by larger (1Φ) grain sizes with higher fall velocities (greater than 8.5 cm s⁻¹). One explanation for this unanticipated correlation between clams and similarly sized sediment grains, is that their transport and deposition is dominated by their diameter rather than their fall velocity. This might be the case if they were transported as bedload, rather than suspended load, because bedload transport is a function of particle diameter, as well as fall velocity and specific gravity (Yalin 1977).

To assess whether gem clams were transported as bedload, the ratio of their settling velocity (w: κu_* , where $\kappa = 0.4$) was used to estimate the relative importance of suspended versus bedload transport for clams. When this nondimensional parameter is significantly greater than 1, a dramatic reduction in the amount of suspended load occurs (Yalin 1977). At our study site, this ratio ranged from 2.5 to 107, indicating that most of the clams were probably not transported in suspension. Thus, it is likely that the clams were transported as bedload, and possible that the correlation between clam transport and 1Φ sediments was due to their similar behavior during bedload transport. Note, however, that hydrodynamic processes other than those occurring on flood tides or on the particular dates we measured could have been responsible for sediment distributions, and this alternate possibility cannot be excluded by our observations.

Recent flume and field studies of several species of bivalve larvae have shown that bedload transport is often an important process during larval settlement and post-settlement movements. Jonsson et al. (1991) showed that although larvae of the cockle, *Cerastoderma edule*, swam up off the bottom in still water and slow flume flows, they were restricted to the viscous sublayer in moderate flows

(5-10 cm s⁻¹) and were transported strictly as bedload in faster flows (15 cm s⁻¹). An exhaustive field study by Emerson and Grant (1991) demonstrated that bedload transport of the soft-shelled clam, Mya arenaria, was responsible for the widespread redistribution of large quantities of individuals, and accounted for much of the variability in population densities of an exposed sandflat. The observation that juvenile G. gemma may be transported as bedload, rather than suspended in the water column can explain why Sanders et al. (1962) found gem clams associated with coarser sands than expected in Barnstable Harbor, and why very few gem clams were collected in plankton nets by Green and Hobson (1970). Thus, active behaviors, such as those described in Grant (1981) and Palmer (1984) for some benthic meiofauna, need not be invoked to explain the transport and deposition of gem clams in Little Buttermilk Bay.

The distributions of three sediment size classes $(1\Phi, 2\Phi, \text{ and silt-clay})$ under the wake support the idea that flood-tide flows are influencing transport and deposition of sediments as well as gem clams in the headland wake. The coarse sand grain class (1Φ) was most prominent in stations along the channel, bordering the sand spit. Velocities observed near the channel were stronger than those in the middle of the mudflat, and currents appeared to carry only the finer particles toward the eddy center. Shear velocities in the wake were nowhere strong enough to keep 1Φ grains (minimum $u_{*crit} = 1.63 \text{ cm s}^{-1}$) in suspension, and could resuspend 2Φ grains (minimum $u_{*crit} = 0.67$ cm s⁻¹) only at a few stations along the perimeter. This pattern was reflected in the significant (p < 0.05) negative Spearman's correlation between perpendicular distance from the channel and 1Φ grains (Table 3). The significant positive correlation between perpendicular distance from the channel and silt-clay suggests that fine sediments remain in the water column long enough to be transported into the wake interior.

Correlations between transported *G. gemma* and resident adults were calculated to explore the extent to which transport of juvenile *G. gemma* may have influenced their recruitment into resident adult populations. Adults were generally more abundant along the sandspit than elsewhere in the wake (Fig. 6), and were positively (but significantly only on July 25) correlated with transported juveniles. These results suggest that although transport of juveniles in the flood-tide headland wake may form aggregations of recruits, subsequent processes may modify their distributions slightly. One possibility is that juveniles are resuspended and redistributed on ebb tides, so that no net accumulation occurs in the wake. For this to occur, the ebb-tide

shear velocities at the site would have to exceed the critical erosion velocities of the clams. We believe this is unlikely, except perhaps near the channel, but additional velocity measurements are necessary to exclude the possibility. Additional deposition of juveniles on the ebb tide from sources further inside Little Buttermilk Bay is also unlikely because the rest of the bay is shallower and experiences lower velocities than the channel near the study site (Fish 1987). A more likely scenario is that some of the adults are occasionally resuspended. For example, on August 19, 1991, Hurricane Bob swept through the study site and the strong winds and storm surge may have redistributed the adult G. gemma population. The similarity between juvenile transport patterns and adult distributions, even after this hurricane, however, supports the idea that episodic transport of adults modifies their distributions, but does not obscure the patterns generated by accumulation of juveniles. Aside from storm conditions, more subtle biological factors such as predation, intraspecies and interspecies competition, in-situ reproduction, or migration in response to sediment grain size or pore-water composition may all significantly alter the resident population density and distribution. Although none of these processes can be definitively excluded from consideration when explaining gem clam distributions, the results of the present study strongly suggest that hydrodynamic transport processes play a dominant role.

In summary, although flows in the headland wake at Lewis Point did influence gem clam transport, they did not do so in the manner predicted by Kellogg (1905). Flows in the wake interior were too weak to transport and accumulate gem clams in a bottom convergence. Instead, the gem clams were deposited just inside the wake perimeter, where the eddy shear velocities dropped to below the clams' critical erosion velocity. This result demonstrated that accumulation in a coastal flow separation can occur even in the absence of a welldefined eddy or a strong bottom convergence. Coarse sediment grains with diameters (but not fall velocities) similar to clams were also found along the wake periphery. The relatively slow velocities throughout the headland wake suggest that both the coarse grains and the immature clams were being transported as bedload, rather than suspended in the water column. Particle diameter appears to be a dominant factor controlling bedload transport in this flow regime. Adult gem clam populations tended to be locally abundant in regions receiving transported juveniles, but clam transport on any specific flood tide was not sufficient to fully predict the adult distributions.

ACKNOWLEDGMENTS

We are grateful to E. D. Garland for assistance in the field and laboratory. Discussions with M. S. Bruno, J. F. Grassle, R. P. Signell, and J. H. Trowbridge were helpful throughout the project. Versions of this manuscript were improved by comments from J. F. Grassle and two anonymous reviewers. Financial support was provided by Office of Naval Research grant N00014-89-J-1431 to L.S.M. and a Woods Hole Oceanographic Institution Summer Student Fellowship to K.L.R. This work is, in part, the result of research sponsored by National Oceanic and Atmospheric Administration, National Sea Grant College Program Office, Department of Commerce, under grant no. NA90-AA-D-SG480, Woods Hole Oceanographic Institution Sea Grant Project no. R/B-104. The United States Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon. Contribution number 8194, Woods Hole Oceanographic Institution.

LITERATURE CITED

- BOWDEN, K. F. 1981. Turbulent mixing in estuaries. Ocean Management 6:117–135.
- BUTMAN, C. A. 1987. Larval settlement of soft sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanography and Marine Biology Annual Review 25:113– 165.
- CLAUSER, F. H. 1956. The turbulent boundary layer. Advances in Applied Mechanics 4:1–51.
- EMERSON, C. W. AND J. GRANT. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnology and Oceanography* 36: 1288–1300.
- FISH, C. B. 1987. Computer enhanced modelling of tidal velocities and circulation patterns, Buttermilk Bay, Massachusetts: A model study and development of methods for general application. Hydrological Research Group, Department of Geology, Boston University, Boston Massachusetts. Technical Report 9.
- FOLK, R. L. 1974. Petrology of Sedimentary Rocks. Hemphill, Austin, Texas.
- GEYER, W. R. 1993. Three-dimensional tidal flow around headlands. Journal of Geophysical Research 98:955-966.
- GRAF, W. H. 1971. Hydraulics of Sediment Transport. McGraw-Hill, New York.
- GRANT, J. 1981. Sediment transport and disturbance on an intertidal sandflat: Infaunal distribution and recolonization. *Marine Ecology Progress Series* 6:249–255.
- GREEN, R. H. AND K. D. HOBSON. 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). *Ecology* 51:999–1011.
- HANNAN, C. A. 1984. Initial settlement of marine invertebrate larvae: The role of passive sinking in a near-bottom turbulent flow environment. Ph.D. Dissertation, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts. Technical Report 84-18.
- JACKSON, J. B. C. 1968. Bivalves: Spatial and size-frequency distributions of two intertidal species. *Science* 161:479–480.
- JACOBSEN, T. R., J. D. MILUTINOVIC, AND J. R. MILLER. 1990. Recruitment in estuarine benthic communities: The role of physical processes, p. 513–525. *In* R. T. Cheng (ed.), Residual Currents and Long-term Transport. Coastal and Estuarine Studies, Vol. 38. Springer Verlag, New York.
- JONSSON, P. R., C. ANDRÉ, AND M. LINDEGARTH. 1991. Swimming behavior of marine bivalve larvae in a flume boundary-layer flow: Evidence for near-bottom confinement. *Marine Ecology Progress Series* 79:67–76.

- KALKWIJK, J. P. T. AND R. BOOIJ. 1986. Adaptation of secondary flow in nearly-horizontal flow. *Journal of Hydraulic Engineering* 24:19–37.
- KELLOGG, J. L. 1905. Conditions governing the existence and growth of the soft-shelled clam (*Mya arenaria*). Report of the Commissioner for the year ending June 30, 1903. United States Commission of Fish and Fisheries, Part 29, p. 195–224.
- NATIONAL OCEANOGRAPHIC AND ATMOSPHERIC ADMINISTRATION. 1990. Nautical Chart 13229: South Coast of Cape Cod and Buzzards Bay, Massachusetts. United States Department of Commerce, Washington, D.C.
- PALMER, M. A. 1984. Invertebrate drift: Behavioral experiments with intertidal meiobenthos. *Marine Behavior and Physiology* 10: 235–253.
- PALMER, M. A. 1988. Dispersal of marine meiofauna: A review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Marine Ecologi*cal Progress Series 48:81–91.
- PINGREE, R. D. 1978. The formation of the shambles and other banks by tidal stirring of the seas. *Journal of the Marine Biological Association of the United Kingdom* 58:211–226.
- SANDERS, H. L. 1958. Benthic studies in Buzzards Bay. I. Animalsediment relationships. *Limnology and Oceanography* 3:245–258.
- SANDERS, H. L., E. M. GOUDSMIT, E. L. MILLS, AND G. E. HAMP-SON. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnology and Oceanography* 7:63–79.

- SELLMER, G. P. 1967. Functional morphology and ecological life history of the gem clam, *Gemma gemma* (Eulamellibranchia: Veneridae). *Malacologia* 5:137–223.
- SIGNELL, R. P. AND W. R. GEYER. 1991. Transient eddy formation around headlands. *Journal of Geophysical Research* 96:2561– 2575.
- SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Co., San Francisco.
- TURNER, H. J. 1953. A review of the biology of some commercial molluscs of the east coast of North America. Sixth Report on Investigations of the Shellfisheries of Massachusetts, p. 39–74. Commonwealth of Massachusetts, Department of Natural Resources, Division of Marine Fisheries, Boston, Massachusetts.
- WEINBERG, J. R. 1985. Factors regulating population dynamics of the marine bivalve *Gemma gemma*: Intraspecific competition and salinity. *Marine Biology* 86:173–182.
- WOLANSKI, E. AND W. M. HAMNER. 1988. Topographically controlled fronts in the ocean and their biological influence. Science 241:177–181.
- WOLANSKI, E. J. I. AND M. HERON. 1984. Island wakes in shallow coastal waters. *Journal of Geophysical Research* 89:10,553–10,569.
- YALIN, M. S. 1977. Mechanics of Sediment Transport, 2nd edition. Pergamon Press, Oxford.

Received for consideration, October 29, 1993 Accepted for publication, March 1, 1994